Invertebrate Reproduction and Development, 47:1 (2005) 63–72
Balaban, Philadelphia/Rehovot
0168-8170/05/$05.00 © 2005 Balaban

The early life history of *Sesarma fossarum*, an endemic freshwater crab from Jamaica

KLAUS ANGER
Biologische Anstalt Helgoland, Stiftung Alfred-Wegener-Institut für Polar- und Meeresforschung, 27498 Helgoland, Germany
Tel. +49 (4725) 819348; Fax +49 (4725) 819369; email: kanger@awi-bremerhaven.de

Received 9 December 2004; Accepted 30 March 2005

Summary

The freshwater crab *Sesarma fossarum* (Decapoda, Brachyura, Sesarmidae) was only recently described as a new species. As in most other endemic Jamaican crabs that have radiated in limnic and terrestrial environments, its early life history has been largely unknown. In an experimental laboratory study this species was reared through embryonic, larval, and early juvenile development, and ontogenetic changes in biomass (contents of carbon, nitrogen, and hydrogen) were measured. The duration of egg development varied greatly within a single brood, such that larval hatching occurred through an extended period (12 d). Larval development invariably consisted of two non-feeding (fully lecithotrophic) zoeal stages and a facultatively lecithotrophic megalopa, followed by metamorphosis to the first juvenile crab stage (always feeding). The zoeal phase lasted on average 4–5 d, while the megalopa required 8–10 d. This abbreviated and largely food-independent mode of development is interpreted as a life-history adaptation to conditions of food limitation in the breeding habitat of this species (presumably maternal burrows dug in river banks). This strategy is based on an enhanced maternal energy investment in the production of large, yolk-rich eggs (ca. 1.4 mm size, 0.6–0.7 mg dry mass). The megalopa shows a highly flexible nutritional strategy where the appearance of a functional feeding system allows for exploitation of external energy sources, while its development remains, in principle, independent of scarcely available food. However, when megalopae were reared without any food, the first juvenile crab stage showed an enhanced mortality and a reduced body size. Decreasing C, H, and C:N values indicate that the fully endotrophic (embryonic and zoeal) phase is principally based on a utilization of lipid reserves; the same applies to the development of megalopae reared in a continued absence of food. In fed megalopae, increasing N and decreasing C:N values indicate that dietary energy was primarily invested in protein synthesis, required for the construction of new tissues and organs. Similarity in the reproductive, developmental, and bioenergetic traits of *S. fossarum* and other limnic or terrestrial crabs from Jamaica suggest that food limitation during the early larval phase has been one of the principal selection factors driving the evolution of the endemic non-marine clade of sesarmids towards increasing egg size and larval lecithotrophy.

Key words: Crustacea, Decapoda, Brachyura, Sesarmidae, larval development, adaptive radiation, lecithotrophy, limnic, bioenergetics, CHN

Introduction

With its high number of endemic animal and plant species, the Caribbean island of Jamaica is known as a hot spot of tertiary and quarternary evolution. Since its emergence from the sea about 28 Myr ago, there have been numerous events of marine colonization; in several cases these were followed by processes of adaptive radiation on land and in freshwater, for instance in frogs, lizards and, more recently, in sesarmid crabs (Hedges, 1996; Schubart et al., 1998, Graham, 2003). In the latter case, morphological and molecular genetic evidence indicates consistently that various limnic and terrestrial species have evolved from a single coastal marine ancestor, which was very closely related to an extant mangrove-dwelling crab species, *Sesarma curacaoense* Rathbun 1897 (see Hartnoll, 1964; Schubart et al., 1998; Schubart and Koller, 2005).

Comparative life-history studies of those endemic species should be particularly rewarding for the understanding of limnic and terrestrial invasions, as well as for that of adaptive radiations in general, because the early (by origin marine planktonic) life-cycle stages are especially sensitive against typical non-marine environmental stress factors such as desiccation, planktonic food limitation, and strong variability in temperatures or ion concentrations (for recent review, see Anger, 2001, 2003). Since the first discoveries of endemic Jamaican crabs by Benedict (1892) and Rathbun (1896), studies have been conducted on the morphological description of new species (Rathbun, 1914; Hartnoll, 1971), and to studies of their ecology, reproduction, regional distribution, and adult behaviour (see Hartnoll, 1964; Abele and Means, 1977; Diesel and Horst, 1995; Diesel 1997, and papers cited therein).

Until recently, only five endemic terrestrial and freshwater-dwelling species of sesarmid crabs were known from Jamaica. Using detailed analyses of morphometric, ecological and distributional patterns, in combination with novel molecular genetic techniques, five new limnic species have recently been identified, raising the total number of presently known endemic sesarmid species to 10 (see Schubart et al., 1998; Schubart and Koller, 2005), and a few additional species are likely to be described in the near future (Schubart, pers. comm.).

Among these endemic crab species, the early life history has been investigated in some detail only in the "bromeliad crab", *Metopaulias depressus* Rathbun 1896. This terrestrial species is mostly associated with bromeliad plants growing on forest-covered limestone hills in central northern Jamaica. A pioneering study by Hartnoll (1964) showed that this crab has no direct mode of development, as could have been expected from its life style, but a complex life-cycle with a free-living larval phase. This includes two zoeal stages and a megalopa, which develop in small rainwater reservoirs collected in leaf axils of large bromeliads (Hartnoll, 1964). The reproductive success of *M. depressus* in this unusual habitat is aided by maternal brood protection behaviour (see Diesel, 1997, and references therein). Moreover, the first rearing experiments carried out under controlled laboratory conditions (Anger and Schuh, 1992) provided physiological and biochemical evidence for far-reaching adaptations in the reproduction and early life history of this crab: its two zoeal stages are non-feeding (i.e., fully lecithotrophic and completely independent of food), while the megalopa begins to eat when food is available, but its development to metamorphosis is still, in principle, independent of exogenous energy sources (facultative lecithotrophy).

Compared with the life histories of typical marine sesarmid crab species, the mode of larval development in *M. depressus* is abbreviated and nutritionally highly flexible (for review, see Rabalais and Gore, 1985; Anger, 1995b). However, it resembles its closest relative living in brackish coastal mangrove habitats on Jamaica, *Sesarma curacaoense*, in that the larval phase is also comprised of two zoeal stages and a megalopa (Anger et al., 1995), with a pronounced tendency towards larval lecithotrophy (Anger, 1995a). This suggests that these unusual early life-history patterns represent ancestral traits that were already present in the colonizing marine species that gave rise to the adaptive radiation of crabs on this island.

A similar mode of development as in *M. depressus* and *S. curacaoense* may therefore be expected to occur also in the other endemic sesarmid crab species (all assigned to the genus *Sesarma*). This hypothesis is corroborated by large egg size found in all species for which data have become available (for references, see Anger, 1995b, 2001; Anger et al., 1995; Diesel et al., 2000), and by observations of large and yolky first-stage zoea larvae in *S. bidentatum* Benedict 1892 (see Hartnoll, 1964), *S. jarvisi* Rathbun 1914 (see Abele and Means 1977), and *S. fossarum* Schubart et al. 1997 (see Anger and Schubart, 2005). Except for these preliminary observations, however, the early life histories of the endemic Jamaican species of *Sesarma* have remained largely unknown.

The first experimental life-history data were provided only very recently by Anger and Schubart (2005), showing that two limnic species, *S. windsor* Türkay and Diesel 1994 (redescribed by Schubart et al., 1997) and *S. dolphinum* Reimer et al. 1998, have, in fact, very similar developmental traits as the

terrestrial crab *M. depressus*, passing through two completely non-feeding zoeal stages and a facultatively lecithotrophic megalopa to the first juvenile crab stage. The present study presents the first experimental evidence for a similar pattern of larval development in another freshwater-breeding crab species from Jamaica, *S. fossarum*.

Materials and Methods

Collection and maintenance of crabs

S. fossarum, including one ovigerous female (body size: 20.0 mm carapace width), were collected on two occasions in March 2004 from the upper Martha Brae River, next to Windsor Cave, Cockpit Country (Trelawny, Jamaica). Five eggs were removed from the ovigerous female and stored frozen at −18°C for later determinations of biomass and chemical composition (see below). The crabs were transported to the Discovery Bay Marine Laboratory (Discovery Bay, St. Ann) and subsequently maintained in freshwater kept at 24 ± 3°C and a natural light cycle. Plant materials collected from the Martha Brae river were given as natural food sources. Later, the crabs were transported to the Helgoland Marine Biological Laboratory (Germany) where they were maintained in aquaria with aerated tap water and limestones with crevices that were added as a calcium source and as a substrate allowing the crabs to hide or to climb emersed in the air. The conditions of temperature (24 ± 1°C) and light were kept similar as in Jamaica (12:12 h L:D cycle). Frozen isopods and grated carrots were provided as food. The ovigerous female was checked at least twice daily for the occurrence of freshly hatched larvae. Hatching began in April 2004.

Larval rearing and sampling

Within 12 h after hatching, the larvae were transferred with wide-bore pipettes to individual 100 ml Nunc™ plastic bowls filled with freshwater previously stored in a container with limestones. No aeration was provided. The conditions of temperature and light were the same as in the maintenance of adult crabs. Larval cultures were checked every 12 h, and moults or mortality were recorded. Water was changed every 24 h.

Behavioural observations (see Results section) consistently indicated that the zoeae were entirely non-feeding, while the megalopa exhibited searching and feeding behaviour as a response to offered food (brine shrimp nauplii). No food was thus given throughout the zoeal phase, while the megalopae were routinely fed daily with freshly hatched *Artemia* sp. nauplii (density ca. 10–15/ml). Before the nauplii were added to larval cultures, they were carefully rinsed with freshwater on a sieve (100 µm mesh size) to remove adherent salts.

In the megalopa stage, it was also tested if the presence or absence of food (*Artemia* nauplii) affected the survival, time of development to metamorphosis, or changes in body mass and chemical composition. One group (13 individuals) was reared from hatching to metamorphosis without any food supply. Near the end of the megalopa stage (on day 8 of its moulting cycle, immediately after the onset of metamorphosis to the first juvenile crab stage), four unfed individuals were sampled and sacrificed for later determinations of dry mass and contents of carbon, hydrogen and nitrogen (collectively referred to as CHN; see below). Another set of four replicate CHN samples was taken from a group of 8-d-old megalopae that had been reared with food. The remaining individuals were used for determination of development time and survival through metamorphosis in presence or absence of food.

Measurements of body size, biomass and elemental composition (CHN)

Juvenile body size was measured to the nearest 0.01 mm as carapace width (CW) between the tips of the posterior lateral carapace spines (see Fig. 1 in Schubart et al., 1997), using a Leica MZ8 stereomicroscope equipped with a calibrated eye-piece micrometer. Adult body size (same dimension) was measured to the nearest 0.1 mm with a Vernier caliper.

Changes in biomass (measured as dry mass, W, and CHN per individual) and elemental composition (CHN in % of W; C:N, C:H mass ratios) were studied during completely endotrophic development from hatching to metamorphosis (i.e., in larvae reared without food), as well as in megalopae reared with food (*Artemia*). First samples were taken within a few hours after hatching, then again at the end of zoeal development, and shortly before metamorphosis from the megalopa to the first juvenile crab stage (for development durations, see Fig. 1B).

Another female which had been collected in 2003 during a previous study on Jamaica (Anger and Schubart, 2005), and then kept in an aquarium at Helgoland, copulated with a male captured in 2004. Eggs were extruded a few days later (3 April 2004), but the female aborted the egg clutch during the subsequent night. Five of these newly laid eggs were sampled for comparative determinations of CHN (Table 1).

Measurement of dry mass (W) and elemental composition (CHN) followed standard techniques: Samples of individual eggs or larvae were transferred

with wide-bore pipettes to small bowls with distilled water, briefly rinsed, blotted on fluff-free Kleenex paper for optical use, frozen for storage at –20°C in preweighed tin cartridges (with one individual each), freeze-dried in a Lyovac GT-2E vacuum apparatus, weighed to the nearest 0.1 µg on a Mettler UM-3 microbalance, and analyzed for CHN with a Fisons (Carlo Erba) model EA 1108 Elemental Analyzer using acetanilid as a standard. Each analysis of egg or larval W and CHN comprised four or five replicate measurements from single individuals (see Table 1).

Statistical methods

The statistical analyses followed standard techniques (Sokal and Rohlf, 1995), using a JMP (version 3.2.6; SAS Institute Inc.) package. Data are presented as mean values ±1 SD. The data were checked for normal distribution (Kolmogorov–Smirnov test) and homogeneity of variances (Levene's median test). Since no significant deviations were found, Student's *t*-tests were used for comparisons of mean values. Percentage values (CHN in % of W) and ratios (C:N, C:H) were arc-sin transformed prior to statistical analysis.

Results

Embryonic and larval development

The only ovigerous female of *S. fossarum* available for the study of larval development was captured in the field on 20 March 2004. According to microscopical examination, the eggs were in an initial developmental stage, without any signs of embryonic differentiation. However, the precise date of egg extrusion remained unknown, so that the time span from the day of collection of the female until larval hatching represents only the minimum duration of embryonic development. Larval hatching from the same egg clutch occurred during an extended period of almost two weeks (14–26 April 2004). This implies that the duration of embryonic development was highly variable, ranging from at least 25 d to 37 d. In total, 45 larvae hatched during this period, without showing any clear temporal or day–night pattern (Fig. 1A).

The larval development of *S. fossarum* comprised invariably two zoeal stages and a megalopa, followed by metamorphosis to the first juvenile crab instar. All larval stages showed a completely benthic and sluggish behaviour. Only after being mechanically disturbed (e.g., with a forceps or pipette), the zoeae swam a short distance (ca. 1 cm), using abdominal strokes rather than their maxillipedes for locomotion. The megalopae walked exclusively with their pereiopods (i.e., they were never observed swimming with pleopod strokes), responding with rapid escape movements to changes in the conditions of light and shaddow.

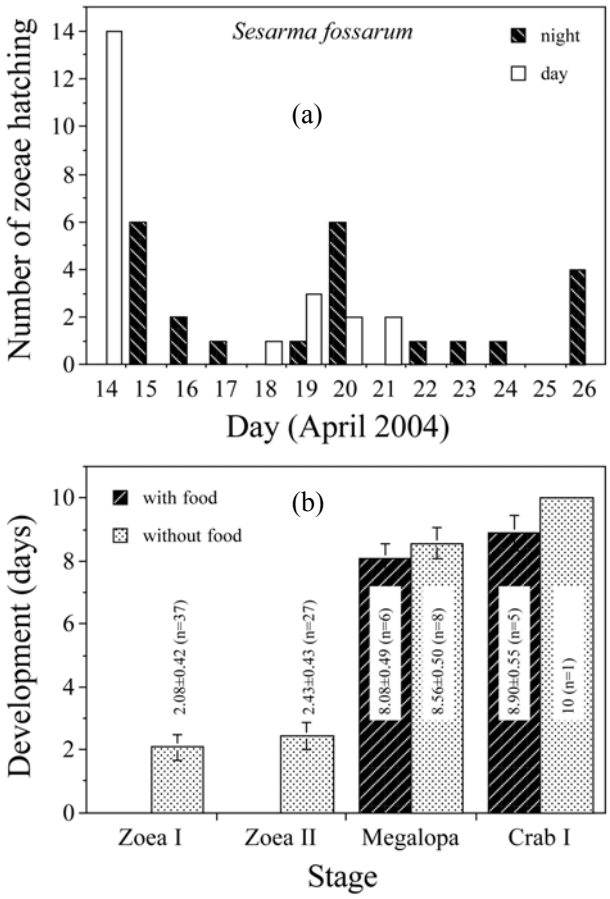

Fig. 1. (a) Hatching pattern. (b) Duration of development through the larval stages (zoea I, II; megalopa, reared with and without food) and the first juvenile crab instar (always fed after metamorphosis, but originating from fed or unfed megalopae, respectively); mean values ±1 SD, number of observations, *n*.

Microscopical observations revealed that the zoeae did not exhibit any positive response to food particles (*Artemia* nauplii, diatoms, or detritus offered in preliminary tests). The megalopae, by contrast, reacted to the presence of food with a conspicuous behaviour of active searching and collecting, in particular with characteristic movements of the pereiopods and mouthparts; an intake of food particles, however, could not clearly be observed with direct microscopical techniques. Hence, it remained initially doubtful if the apparent feeding behaviour of the megalopae was actually associated with an ontogenetic appearance of a functional digestive tract. This was tested with an indirect approach, using as criteria the rates of survival, development and growth in two experimental

groups of megalopae, reared with or without daily food supply.

Larval mortality was generally low, with 100% survival through the zoea-I stage. Three individuals died in the zoea II, and two (1 fed, 1 unfed) died in the megalopa stage. However, the number of individuals was greatly reduced during the experiment due to sampling for determinations of biomass (see below) and for a study of larval morphology (to be published elsewhere). Larval development (at constant 24°C) lasted 1.0–2.5 d in the zoea I stage, 2.0–4.0 d in the zoea II, and 7.5–9.0 d in the megalopa (Fig. 1B). In the latter stage, the average time to metamorphosis was about 0.5 d longer in the group reared in continued absence of food as compared to fed larvae (8.6 d vs. 8.1 d), but this difference was not statistically significant due to low numbers of individuals (n = 6 and 8, respectively) and high variability. The time spent in the megalopa stage alone was thus almost twice the duration of the preceding two zoeal stages combined (4.5 d). Metamorphosis to the first juvenile crab instar was reached 12.5–14.0 d after hatching (mean ± SD: 13.0 ± 0.5 d).

In summary, the presence or absence of food during the megalopa stage had no statistically significant influence on larval survival or development to metamorphosis. However, in the unfed group there was subsequently high mortality in the first juvenile crab stage (which was always fed): seven of eight individuals in this group died within 2 d after metamorphosis, while five out of six crabs in the previously fed group survived, moulting successfully to the second juvenile instar (after 8.0–9.5 d vs. 10 d in the only survivor in the other group; see Fig. 1B). This difference in survival through the first crab stage was statistically significant (Pearson's χ-square statistic = 7.024; P<0.01), indicating a late (postmetamorphic) effect of previous megalopal nutrition. In agreement with this, the body size in the first juvenile crab stage was significantly smaller in the previously unfed group (1.82 ± 0.05 vs. 2.05 ± 0.16 mm CW; t = 3.111; P< 0.02).

Ontogenetic changes in biomass and chemical composition of eggs and larvae

Data of embryonic and larval biomass (W and CHN, all in µg per individual) and chemical composition (CHN in % of W; C:N and C:H mass ratios) are summarized in Table 1. Analyses of eggs in an early stage of embryonic development became available for two clutches, one from the female collected in the field (producing the larvae and juveniles used in this study), another from a female laying eggs in the laboratory. The latter showed significantly (9–13%) lower biomass values compared to the eggs produced in the field. The relative chemical composition, in contrast, varied much less between these two egg clutches, with significant differences (higher values in laboratory-laid eggs) detected only in the percentage values of N (7.8 vs. 7.4) and in the C:H ratio (6.73 vs. 6.61).

During the course of embryonic development, significant amounts of egg biomass were lost. The freshly hatched zoea I larvae (sampled upon hatching on 14 April 2004, i.e., 25 d after the collection of the ovigerous female) had 12% lower W, while the C and H values per individual had decreased by 15% each, and that of N by 10% (see Fig. 2). While the fraction of N (in % of W) and the C:H mass ratio remained stable, the percentage values of C and H as well as the C:N ratio were significantly lower in the zoea I (see Table 1). All together, these changes indicate that the lipid fraction of egg biomass was substantially reduced during the course of embryonic development, while the protein fraction (measured indirectly with the N content and the C:N ratio) was utilized to a much lesser extent.

Similar patterns of change in biomass and relative chemical composition were also found when the freshly hatched zoea I was compared with late zoea II larvae sampled shortly before the moult to the megalopa stage (see Fig. 2). This shows that the two non-feeding zoeal stages combined utilized during their development (lasting in total about 4.5 d; cf. Fig. 1B) approximately equal amounts of organic matter per individual as the embryo during a period of 25 d. Also the proportional patterns of degradation in C, N and H were similar in embryos and zoeae.

Similar patterns were also found in megalopae reared in continued absence of food. Again, significant losses occurred in the fractions of C and H, but not in N (Fig. 2). This was again reflected in a significantly decreasing C:N ratio (from 7.16 to 6.52; Table 1). Hence, also the megalopa utilized lipid reserves rather than proteins as an energy source for food-independent development. However, the percentage rates of biomass loss during the megalopa stage were conspicuously lower than those measured during the preceding zoeal phase (Fig. 2), although the latter lasted only about half as long (cf. Fig. 1B).

In megalopae reared with food, all measures of biomass increased significantly compared to those measured at the end of the zoeal phase (Table 1; Fig. 2). This indicates that great amounts of organic matter from food had been taken up and were successfully converted to larval biomass. On the other hand, successful metamorphosis also occurred in complete

Table 1. *Sesarma fossarum*. Developmental changes in biomass (arithmetic mean values ± 1 SD, *n* = number of replicate measurements): dry mass (W), contents of carbon (C), nitrogen (N), hydrogen (H) (all in µg per egg or larva), elemental composition (C, N, H, in % of W; C:N, and C:H mass ratios); time: days from hatching

Stage	Time (d)	Food	W (µg/ind)		C (µg/ind)		N (µg/ind)		H (µg/ind)		C (%W)		N (%W)		H (%W)		C:N ratio		C:H ratio		
			x	±	*x*	±	*x*	±	*x*	±	*x*	±	*x*	±	*x*	±	*x*	±	*x*	±	n
Egg**			635	79	393	50	49.3	6.4	58.5	7.9	61.9	0.5	7.8	0.1	9.2	0.1	7.98	0.19	6.73	0.05	5
Egg			729	37	446	23	54.1	2.4	67.4	3.7	61.1	0.9	7.4	0.1	9.2	0.1	8.24	0.09	6.61	0.02	5
Zoea I	0	no	641	27	377	17	48.7	1.9	57	2.9	58.9	0.3	7.6	0.1	8.9	0.1	7.74	0.07	6.63	0.04	5
Zoea II	4.5	no	564	35	322	22	44.9	2.2	49.2	3.6	57.1	0.5	8	0.1	8.7	0.1	7.16	0.14	6.55	0.04	5
Megalopa	12	no	572*	52	294*	31	45.1*	3.8	44.3*	5.3	51.4	1.1	7.9*	0.1	7.7	0.2	6.52	0.25	6.65	0.09	4
Megalopa	12	yes	750*	33	391*	17	61.8*	2.3	60*	2.8	52.1	0.2	8.2*	0.1	8	0.1	6.32	0.07	6.52	0.04	4

*Significant differences between biomass of fed and unfed megalopae (t-tests, $P<0.05$).
**Freshly laid eggs from a female kept in the laboratory since 2003; all others values: eggs and larvae produced by another female (collected from the field in March 2004).

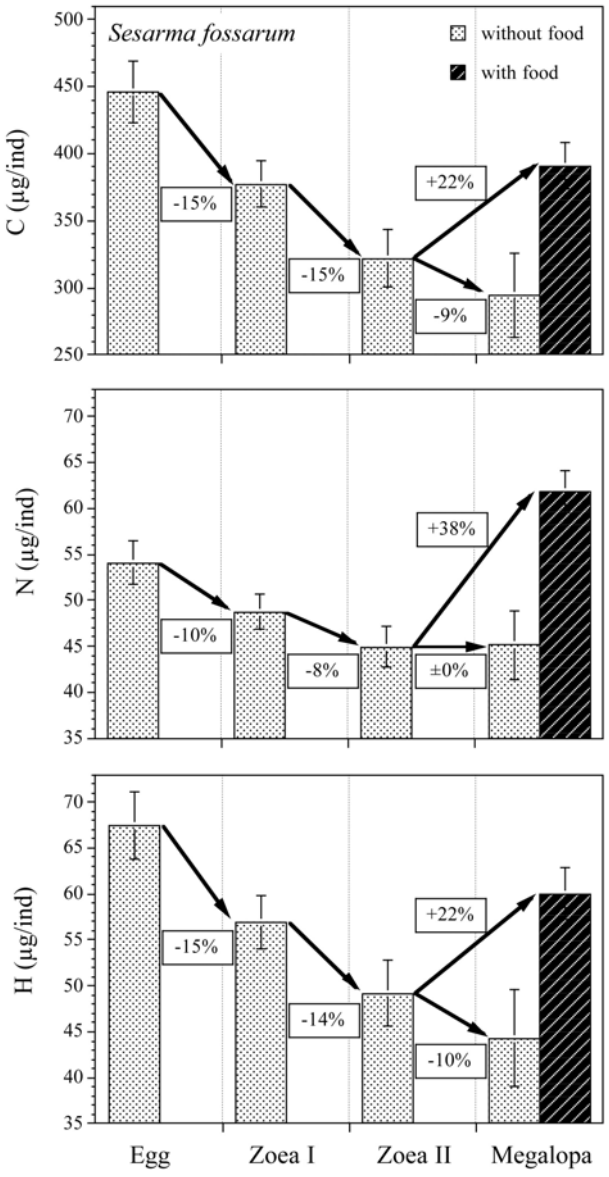

Fig. 2. Changes in carbon (C), nitrogen (N), and hydrogen (H), in µg per individual and as percentage values, during larval development from hatching to metamorphosis (megalopa reared with and without food).

absence of food, indicating that this stage is facultatively lecithotrophic.

When the CHN gains in fed megalopae are compared with the losses during the non-feeding (embryonic and zoeal) phase, or with those occurring during megalopa development in continued absence of food, strikingly different patterns of change become apparent (Fig. 2): In megalopae reared with food, the rate of change in the N content (38% increase) was much greater than the gain in the fractions of C and H (22% each). During endotrophic development, by contrast, the fractions of C and H decreased much more than the N content. The pattern observed in fed megalopae indicates that the nutritional energy was primarily invested in protein synthesis and not in a replenishment of previously lost lipid reserves.

As a net result of all losses and gains occurring during the course of larval development, fed megalopae contained, prior to metamorphosis, only slightly higher amounts of C and H, but about 27% more N (or protein) compared to freshly hatched zoea I larvae. In megalopae reaching metamorphosis under conditions of continued absence of food, by contrast, the values of total W and N (or protein) were about 11% lower than those on the day of hatching, while the contents of C and H had declined by 22% each.

Discussion

Ecological, behavioural, reproductive, and developmental traits

Passing through two rapidly developing and non-feeding (i.e., fully lecithotrophic) zoeal stages and a facultatively lecithotrophic megalopa, *S. fossarum* shows basically the same pattern of postembryonic development as the bromeliad crab, *Metopaulias depressus* (Hartnoll, 1964), and the limnic species *S. windsor* and *S. dolphinum* (Anger and Schubart, 2005). By comparison, most coastal marine sesarmids pass through at least three or four zoeal stages, requiring a total of about 2 weeks (cf. Rabalais and Gore, 1985; Anger, 1995b, 2001). This supports the hypothesis proposed by Anger (2001) that all endemic Jamaican sesarmids may show the same, presumably ancestral, pattern of reproduction and development known from *S. curacaoense* (Anger et al., 1995a), the closest extant coastal marine relative of the limnic-terrestrial clade.

S. fossarum lives in mountain streams in central-northern Jamaica where it digs deep burrows, both below and above the water level, in river banks consisting of strongly consolidated sedimentary soils mixed with limestone formations. The crabs can be observed foraging during daytime both inside and outside the water, hiding rapidly in their burrows when they are disturbed. Aquarium observations showed that this species is omnivorous, eating plant materials as well as meat of various origins (e.g., other crustaceans, fish). Both in their natural habitat and in captivity, the crabs show highly aggressive and territorial behaviour including cannibalism (in the field evidenced by frequent occurrence of limb loss).

The conspicuous aggressive behaviour of this species may have an adaptive value in its particular habitat, where the digging of burrows must be difficult and time-consuming, while the availability of burrows

may be crucial for escape from predation and, presumably, for reproduction. Although we do not know where the larval development of *S. fossarum* actually takes place in nature, our laboratory observations suggest that hatching and subsequent development to metamorphosis should exclusively occur inside the maternal burrows. Outside, the larvae would rapidly be carried downstrem by water currents. Since its larval phase lasts almost 2 weeks (Fig. 1B), larval advection from the habitat of the adults would occur over large distances, most probably reaching the sea. Even if we consider only the zoeae as passively drifting stages (assuming that the megalopae with their well developed walking legs could hide in crevices or cling to benthic substrates on the river banks), 4–5 d of zoeal development in the water column would still imply an irreversible advection. Assuming an average near-bottom current speed of ca. 10 cm/s, they would drift about 30–40 km before reaching the megalopa stage. While a strategy of larval export and later re-immigration is common in estuarine species (Anger, 2001, 2003), this pattern is very unlikely to occur in *S. fossarum* or in other endemic sesarmids on Jamaica because (1) the larvae are very well adapted to freshwater but most probably not to seawater, and (2) small juveniles occur in adult habitats (pers. observ.), which could not have re-immigrated upstream over tens of kilometres without growing to much larger size.

If the larvae of *S. fossarum* develop within the maternal burrows, then we must postulate the occurrence of yet another life-history adaptation in this species. Like the bromeliad crab, *M. depressus* (see Diesel, 1997, and papers cited therein), this species should have evolved maternal brood protection behaviour. Only aggressive territorial behaviour of a mother animal present in the same burrow where larval development takes place can hinder larger juveniles or adult conspecifics to invade the burrow and predate on larvae and early juveniles. Crabs being larger (and potentially stronger) than the mother animal, on the other hand, would not be able to enter its narrow burrow. Furthermore, it is likely that the mother crab also removes decaying debris from the burrow and ventilates the enclosed water body, keeping water quality and oxygen supply at favourable levels, in a similar way as observed in *M. depressus*. It is expected that future field work and/or experimental laboratory studies will scrutinize, and most probably confirm, this likely scenario.

As another peculiar reproductive trait of *S. fossarum*, the duration of embryonic development varies greatly among siblings, so that this species shows an extended period (almost 2 weeks) of larval hatching from a single brood. Similar patterns were observed in the Jamaican congener *S. windsor* (Anger and Schubart, 2005), but also in several species of king crabs (Anomura, Lithodidae) which also have large, lecithotrophic, and mostly sluggish larvae (see Thatje et al., 2003, and references therein). In the latter, extended hatching periods with a low number of larvae hatching per day were interpreted as a strategy facilitating larval escape from visually oriented pelagic predators, which may easily detect and consume conspicuous patches of large and slowly moving larvae. However, if the larval development of *S. fossarum* takes place within maternal burrows, then an extended hatching pattern would, in this case, not be significant as a protection against predators in the water column, but it may reduce benthic predation among conspecific juveniles. Assuming that the early juveniles leave the maternal burrow soon after metamorphosis, living hidden in crevices between rocks or vegetation, or already in small burrows of their own, then these small crabs would exploit other food sources rather than sibling juveniles in the maternal burrow, enhancing the overall level of postmetamorphic survival.

If the reproductive and developmental traits in *S. fossarum* are, as proposed here, in part associated with this species' life in burrows dug in river banks, then we should expect similar characteristics in the congeners *S. windsor* and *S. bidentatum*, which have similar lifestyles as *S. fossarum* (Schubart et al., 1997; Reimer et al., 1998). Future comparative life-history studies in endemic Jamaican sesarmid crabs, including investigations of the relationships between ecological, behavioural, reproductive, and developmental traits, may further enhance our understanding of this adaptive radiation.

Bioenergetic traits

While development inside maternal burrows should effectively protect the larvae of *S. fossarum* against irreversible advection and predation, the early life-history stages should face another serious problem, which probably did not exist in the coastal marine environment of their ancestors. Neither a fast-flowing stream passing through karst highlands in Jamaica nor a stagnant and dark water body enclosed in a crab burrow may allow for sufficient production of planktonic food organisms. For planktotrophic larvae, this would mean nutritional stress. The enhanced female energy investment of *S. fossarum* in the production of large, yolk-rich eggs and larvae may thus be considered as a reproductive adaptation to planktonic food limitation in the breeding habitat. Moreover, the abbreviated and fast mode of zoeal development reduces the time of exposure of the larvae to nutritional stress.

With ca. 1.4-mm diameter and a dry mass of 0.6–0.7 mg, the eggs of *S. fossarum* are similar to those in other endemic Jamaican sesarmids, but they contain 1–2 orders of magnitude more biomass than those of closely related coastal marine species (see Anger, 1995b, 2001, Anger and Schubart, 2005). Also the C:N mass ratios of the eggs and freshly hatched zoeae are significantly higher in *S. fossarum* (ca. 7.7–8.2), indicating large lipid stores. Equipped with these energy reserves, the zoeae are perfectly adapted to survive and develop under conditions of complete lack of suitable food. Therefore, they do not even develop functional feeding appendages (Thatje and Anger, in prep.) nor any behavioural response to odors from available food, suggesting that their chemoreceptive system may not be functional either.

The energy stores persisting from the egg yolk to the megalopa stage are reduced compared to those present on the day of hatching, but still sufficiently high to provide continued nutritional independence, so that metamorphosis may sucessfully be reached even in complete absence of food. However, if food is continuously lacking, the endotrophic development to metamorphosis implies subsequent costs such as high mortality and reduced body size in the first juvenile crab stage. These late effects indicate an incipient and partial dependence of food in the megalopa stage. In its natural habitat, however, continued lack of food is an unlikely scenario, because the megalopa is fully benthic, shows foraging behaviour, and is equipped with functional walking legs, claws, and other feeding appendages. In the benthos, it should thus normally find some sedimented particles of organic matter including small invertebrates and detritus with adherent microorganisms, so that it must only partially rely on its internal energy stores.

In summary, the megalopa of *S. fossarum* is nutritionally highly flexible, being in principle independent of food, but also capable of exploiting external energy sources. When sufficient food is available, it becomes the first postembryonic stage that exhibits growth, with biomass accumulation compensating or exceeding previous losses (see Fig. 2). Interestingly, however, the nutritional energy is not primarily utilized for the replenishment of previously lost lipid reserves, but preferentially invested in new proteinaceous structures (indicated by a particularly strong increase in the N fraction of biomass and a significant decrease in the C:N ratio of fed megalopae; see Table 1). The new proteins are probably accumulated mainly in nervous tissues and musculature, which are increasingly required for metamorphic changes in functional morphology and behaviour. Moreover, the content of total CHN within W decreased significantly from 73.8% at the end of zoea II stage to 67.0–68.3% in starved and fed megalopae, respectively. This indicates a decreasing content of total organic matter and a proportional increase in the inorganic fraction within W, reflecting a rapidly increasing sclerotization of the cuticle, regardless of presence or absence of food. This pattern of change is typical of the brachyuran megalopa, normally corresponding with a change from a planktonic to a semibenthic or benthic life style (Anger, 2001).

The bioenergetic traits of the larval stages of *S. fossarum* resemble previously observed patterns in the terrestrial bromeliad crab, *M. depressus* (Anger and Schuh, 1992), and in the limnic species *S. windsor* and *S. dolphinum* (Anger and Schubart, 2005). This suggests that similar selecting forces may have played key roles in the evolution of these crabs. However, the early life-histories of most other species in the endemic limnic-terrestrial sesarmid clade on Jamaica are still little known, calling for more comparative life-cycle studies. Also, future investigations should analyze regional variation in the ecological conditions prevailing in different river systems and in other habitat types. Together with considerations of palaeo-ecological scenarios (see Graham, 2003), those data will help to identify differential selection pressures and mechanisms of genetic isolation, enhancing our general understanding of the evolutionary processes associated with adaptive radiation and invasions of land and freshwater environments.

In addition to interspecific variations in ecological, reproductive, developmental, and bioenergetic traits, intraspecific variability (including phenotypic plasticity) should be another important issue in future work, as "all evolutionary novelties ultimately arise from intraspecific variation" (Arthur, 2000). In *S. fossarum*, for instance, there seems to be a high degree of variability in egg biomass among broods (Table 1; cf. Anger and Schubart, 2005), which may be associated with variability in embryonic or larval fitness. Under conditions of food limitation, for example, intraspecifically variable energy reserves persisting to the megalopa stage may translate to differential survival and growth in the juvenile phase and, eventually, to variation in reproductive success (cf. Giménez et al., 2004), which should wield different selection pressures under different habitat conditions, and thus, eventually favour the evolution of new species.

Acknowledgements

Thanks are due to Michelina and Tanja for help in the collection, maintenance, and transport of crabs, the

staff of the Discovery Bay Marine Laboratory (St. Ann, Jamaica) for kind hospitality and support, Uwe Nettelmann for technical assistance in the laboratory, and Gabriela Torres, Luis Giménez, and Karin Boos for occasional help in the long-term maintenance of Jamaican crabs on Helgoland. Also, I wish to thank Karin Bickmeyer for rapid and always reliable CHN analyses, Christoph Schubart (Universität Regensburg) for helpful information and stimulating discussions, and an anonymous reviewer who helped to improve the English text of this paper.

References

Abele, L.G. and Means, D.B., *Sesarma jarvisi* and *Sesarma cookei:* montane, terrestrial grapsid crabs in Jamaica (Decapoda). Crustaceana, 32 (1977) 91–93.

Anger, K., Starvation resistance in larvae of a semiterrestrial crab, *Sesarma curacaoense* (Decapoda: Grapsidae). J. Exp. Mar. Biol. Ecol., 187 (1995a) 161–174.

Anger, K., The conquest of freshwater and land by marine crabs: adaptations in life-history patterns and larval bioenergetics. J. Exp. Mar. Biol. Ecol., 193 (1995b) 119–145.

Anger, K., The biology of decapod crustacean larvae. Crustacean Issues 14, A.A. Balkema, Lisse, 2001.

Anger, K., Salinity as a key parameter in the larval biology of decapod crustaceans. Invert. Reprod. Develop., 43 (2003) 29–45.

Anger, K., Schreiber, D. and Montú, M., Abbreviated larval development of *Sesarma curacaoense* (Rathbun, 1897) (Decapoda: Grapsidae) reared in the laboratory. Nauplius, Rio Grande (Brazil), 3 (1995) 127–154.

Anger, K. and Schubart, C.D., Experimental evidence of food-independent larval development in endemic Jamaican freshwater-breeding crabs. Physiol. Biochem. Zool., 78 (2005) 246–258.

Anger, K. and Schuh, M., Bioenergetics of abbreviated larval development in the bromelid crab, *Metopaulias depressus* (Decapoda: Grapsidae). Comp. Biochem. Physiol., 103A (1992) 507–518.

Arthur, W., Intraspecific variation in developmental characters: the origin of evolutionary novelties. Amer. Zool., 40 (2000) 811–818.

Benedict, J.E., Decapod Crustacea of Kingston Harbour. Johns Hopkins Univ. Circ., 11 (1892) 77.

Diesel, R., Maternal control of calcium concentration in the larval nursery of the Bromeliad Crab, *Metopaulias depressus* (Grapsidae). Proc. Royal Soc. Lond. Ser. B – Biol. Sci., 264 (1997) 1403–1406.

Diesel, R. and Horst, D., Breeding in a snail shell: ecology and biology of the Jamaican montane crab *Sesarma jarvisi* (Decapoda: Grapsidae). J. Crust. Biol., 15 (1995) 179–195.

Diesel, R., Schubart, C.D. and Schuh, M., A reconstruction of the invasion of land by Jamaican crabs (Grapsidae: Sesarminae). J. Zool., 250 (2000) 141–160.

Giménez, L., Anger, K. and Torres, G., Linking life history traits in successive phases of a complex life cyle: effects of larval biomass on early juvenile development in an estuarine crab, *Chasmagnathus granulata*. Oikos, 104 (2004) 570–580.

Graham, A., Geohistory models and Cenozoic paleoenvironments of the Caribbean region. Syst. Bot., 28 (2003) 378–386.

Hartnoll, R.G., The freshwater grapsid crabs of Jamaica. Proc. Linn. Soc. Lond., 175 (1964) 145–169.

Hartnoll, R.G., *Sesarma cookei* n.sp., a grapsid crab from Jamaica. Crustaceana, 20 (1971) 257–262.

Hedges, S.B., Vicariance and dispersal in Caribbean biogeography. Herpetologica, 52 (1996) 466–473.

Rabalais, N.N. and Gore, R.H., Abbreviated development in Decapods. In: Larval Growth, Crustacean Issues, Vol. 2, Wenner, A.M. (ed.), A.A. Balkema, Rotterdam, 1985, pp. 67–126.

Rathbun, M.J., Description of a new genus and four new species of crabs from the West-Indies. Proc. U.S. Nat. Mus., 19 (1896) 141–143.

Rathbun, M.J., New genera and species of American Brachyrhynchous crabs. Proc. US Natl. Mus., 47 (1914) 117–129.

Reimer, J., Schubart, C.D. and Diesel, R., Description of a new freshwater crab of the genus *Sesarma* Say, 1817 (Brachyura, Grapsidae, Sesarminae) from Western Jamaica. Crustaceana, 71 (1998) 185–196.

Schubart, C.D., Diesel, R. and Hedges, S.B., Rapid evolution to terrestrial life in Jamaican crabs. Nature, 393 (1998) 363–365.

Schubart, C.D. and Koller, P., Genetic diversity of freshwater crabs (Brachyura: Sesarmidae) from central Jamaica with description of a new species. J. Nat. Hist. 39 (2005) 469–481.

Schubart, C.D., Reimer, J., Diesel, R. and Türkay, M., Taxonomy and ecology of two endemic freshwater crabs from western Jamaica with the description of a new *Sesarma* species (Brachyura: Grapsidae: Sesarminae). J. Nat. Hist, 31 (1997) 403–419.

Sokal, R.R. and Rohlf, F.J., Biometry. The Principles and Practice of Statistics in Biological Research. Freeman, San Francisco, 1995.

Thatje, S., Calcagno, J.A., Lovrich, G.A., Sartoris, F.J. and Anger, K., Extended hatching periods in the subantarctic lithodid crabs *Lithodes santolla* and *Paralomis granulosa* (Crustacea: Decapoda: Lithodidae). Helgol. Mar. Res., 57 (2003) 110–113.